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Key points

1. Biogeographical patterns of ferns and angiosperms are the result of a combination of vicariance and long distance dispersal, but due to their more effective dispersal via spores, the latter is more frequent among ferns. Therefore, fern species tend to have wider ranges and the relative number of fern species compared with seed plants is highest on remote, mountainous tropical islands such as Hawaii and the Mascarenes. Also, fern communities on different continents are more similar compositionally than those of seed plants.
2. Despite their potential for long distance spore dispersal, many fern species have localized ranges as a result of low frequency of successful long distance dispersal, habitat specialization, geographical isolation and competitive interactions between species.
3. Species richness of ferns follows a latitudinal gradient that peaks in the tropics, where ferns are especially diverse and abundant in wet habitats with moderate temperatures at elevations of about 1000–2500 m. On average, species in tropical mountains have elevational amplitudes of about 1000 m. The peak of endemism is located at higher elevations than that of species richness.

2.1 Introduction

Biogeography deals with the distribution patterns of species and communities, and their causal relationships with factors such as climate, soil and evolutionary history (Humboldt, 1805; Lomolino *et al.*, 2006). Specific topics addressed by biogeographers include the sizes of geographical ranges and their spatial placement, the way individual species attain their distribution ranges (dispersal, extinction and vicariance), the distribution of species numbers (alpha diversity), changes in species composition (beta diversity) and the spatial distribution of species traits (macroecology). These aspects can be addressed at different spatial and temporal scales, ranging from global to local and focusing on the present-day situation as well as on past conditions.

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Ferns have long been the subject of biogeographical studies (e.g., Christ, 1910), but many of these topics have only been dealt with cursorily or within a specific geographical or ecological context that has not previously permitted general conclusions. From a biogeographical point of view, ferns are primarily distinguished from flowering plants by their spore dispersal and their separate gametophytic and sporophytic generations. Accordingly, they are independent of biotic pollination and distribution vectors (with few exceptions such as aquatic ferns transported by waterfowl), eliminating two of the aspects that strongly influence flowering plant biogeography, resulting in a closer biogeographic relationship to climate and substrate (Barrington, 1993; Given, 1993). In addition, ferns are particularly suitable organisms for biogeographic studies because of their worldwide distribution, as well as their moderately high but manageable species richness that allows for both quantitative sampling and statistical inference (Tuomisto, 1994; Kessler and Bach, 1999). Additionally, the occurrence of independent gametophytic and sporophytic generations in ferns (see Chapter 3) allows a direct comparison of "moss-like" and "angiosperm-like" forms within the same taxon and hence might serve as models on how land plants have evolved and adapted to their new environment.

2.2 Dispersal and vicariance

2.2.1 Long distance dispersal

Dispersal of fern (and lycophyte) species takes place primarily via dust-like spores, although some species produce gametophytic gemmae also suitable for medium distance dispersal (Dassler and Farrar, 2001), or vegetative buds (Plate 5A) and rhizomes from sporophytes as well as sporocarps in aquatic species that mainly serve for short distance dispersal. Single fern individuals may produce millions of spores, and while most of them only disperse a few meters (Conant, 1978; Wolf *et al.*, 1991; Sheffield, 1996), dispersal over thousands of kilometers is possible (Tryon, 1985; Barrington, 1993; Smith, 1993; Schneller and Liebst, 2007). The latter presumably takes place mainly via air currents at intermediate (e.g., trade winds, storm systems) to high (e.g., jet streams) altitudes (Erdtman, 1937; Polunin, 1951; Gressitt *et al.*, 1961; Punetha, 1991; Caulton *et al.*, 2000), although direct experimental evidence for this is still lacking. However, the ability of bryophyte and fern spores to survive extreme environmental conditions in the high atmosphere (e.g., low temperatures, high ultraviolet radiation) has been experimentally demonstrated (Gradstein and van Zanten, 2001).

Long distance dispersal events are rare but disproportionately important in determining the distribution patterns of fern species (Renner, 2005; Nathan, 2006). Factors influencing the potential for long distance dispersal among ferns

have never really been addressed by specific studies. Small spore size (20–100 μm in diameter), and the ability of a number of species to be apogamous or to produce bisexual gametophytes capable of self-fertilization (see Chapter 3), certainly play an important role (Tryon, 1970, 1976; Smith, 1972, 1993; Wolf *et al.*, 2001). Spores vary in size, shape, and surface ornamentation (see Chapter 1; Tryon and Lugardon, 1990), but these traits may be unimportant in dispersal because at the scale of spore size the laws of fluid mechanics apply. A different relationship is presented by epiphytic species with long-lived, colonial, gemmiferous gametophytes (e.g., grammitid, filmy and vittarioid ferns, Dassler and Farrar, 1997, 2001). While there is no direct evidence for long distance dispersal by gemmae, because all these species also produce spores, ferns with such gametophytes are relatively more abundant on islands than on continental land areas (Dassler and Farrar, 2001), and are over-represented among species pairs or putative species pairs shared between the neotropics and Africa/Madagascar (Moran and Smith, 2001; Janssen *et al.*, 2007). Whether this is due to a higher probability of arrival or a higher probability of successful establishment remains to be explored.

Yet another comparison related to dispersal can be made between spores with and without chlorophyll. Some fern groups such as Equisetaceae (Plate 4C), grammitid ferns, Hymenophyllaceae (Plate 6A, B), Onocleaceae, and Osmundaceae, have green spores that are presumably more vulnerable to climatic extremes (e.g., drought, frost) and are shorter lived (48 days on average) than spores without developed chloroplasts that may survive for months to years (see Chapter 1; Lloyd and Klekowski, 1970). Accordingly, such species may be less capable of long distance dispersal and hence they should have smaller ranges. While they should therefore be underrepresented on islands, such a tendency has been observed to be weak (Kessler, 2002b). This distribution pattern suggests that even short-lived, chlorophyllous spores are viable long enough to achieve very broad ranges (e.g., *Melpomene flabelliformis* ranging from the Andes to the Mascarenes; *Hymenophyllum polyanthos*, a filmy fern of pantropical distribution). A lack of correlation between range size and presence of chlorophyll in spores has also been found among tropical liverworts, which have comparable spore sizes (van Zanten and Gradstein, 1988).

2.2.2 Dispersal to oceanic islands

The potential for long distance dispersal among ferns is best illustrated by oceanic islands that have never been connected to the mainland and thus can only be colonized via long distance dispersal (Tryon, 1985; Barrington, 1993; Smith, 1993). The best studied island system is Hawaii, located approximately 4000 km from the nearest continent. This island chain is about 85 million years old, but

erosion and subsidence of older islands imply that the current terrestrial biota could not have colonized the islands prior to about 23 million years ago (mya; Price and Clague, 2002). The Hawaiian Islands are inhabited by 188 species of native ferns, of which 77% are endemic (Palmer, 2003). Taxonomic and phylogenetic studies suggest that these species are the result of at least 140 independent colonization events (Wagner *et al.*, 1990; Wagner, 1995), although this number is likely to be an underestimate, because one species alone, *Asplenium adiantum-nigrum* (black spleenwort), may have colonized the Hawaiian Islands at least three times and perhaps as many as 17 times (Ranker *et al.*, 1994; but see Vogel *et al.* 1999a). In a review of phylogenetic studies of six Hawaiian fern genera, Geiger *et al.* (2007) showed that at least 11 independent colonization events have occurred. Six or seven of these lineages are related to southern Pacific or Southeast Asian clades and probably arrived in Hawaii via the subtropical jet stream, a high-altitude wind current. Other lineages arrived from the New World either via the trade winds or in storm systems acting at lower altitudes. Once established on Hawaii, several of these lineages underwent adaptive radiations such as the endemic genus *Adenophorus*, related to the widespread *Grammitis*, which has evolved into 11 species (Ranker *et al.*, 2003, 2004). In the genus *Diellia*, there is evidence for island chain hopping (i.e., the colonization of newly formed volcanic islands from successively older ones; Schneider *et al.*, 2005).

On the Galápagos Islands, another remote volcanic island system that is located about 1000 km west of South America, a preliminary study by Adersen (1988) suggests that the species composition of fern and lycophyte communities on the islands corresponds to patterns expected from random dispersal events, and that the number of species on the islands is primarily driven by island size, as predicted by the theory of island biogeography (MacArthur and Wilson, 1967). However, detailed phylogenetic analyses are lacking to support this statement.

The capacity of long distance dispersal between continents can be exemplified by the relationships between the neotropics and Africa/Madagascar. Moran and Smith (2001) list 27 species and 87 putative species pairs (i.e., assumed sister species) shared between both continents separated by the Atlantic. With the exception of one example from an old evolutionary lineage (*Anemia*), these putative disjunctions are best explained by long distance dispersal, although superficial similarities between some pairs have proven to be the result of convergence (e.g., Rouhan *et al.*, 2004). Among the derived fern family Polypodiaceae, the mainland African representatives mostly arrived by long distance dispersal from either the neotropics or Asia, with some subsequent speciation (Janssen *et al.*, 2007). Except for perhaps the genus *Platycerium* (staghorn ferns), none of the genera studied by Janssen *et al.* (2007) originated in their host region, Africa.

2.2.3 Vicariance

Long distance dispersal is not the only way in which fern species may attain large and disjunct distribution ranges (Kato, 1993) – that is, ranges that consist of geographically separate parts, either on different islands or continents, or in habitat patches within a geographical region (Fig. 2.1). Such distribution patterns can be explained by three fundamentally different processes: dispersal (see Sections 2.2.1 and 2.2.2), partial extinction from a prior dispersal episode, or vicariance, by which originally contiguous populations are split by geological or climatic changes into separate populations.

In contrast to the numerous examples of long distance dispersal among ferns, undisputed examples for vicariance are rare. This is due to the fact that vicariance by continental drift took place such a long time ago that the resulting biogeographic patterns have often been obscured by speciation, extinction and dispersal events (Wolf *et al.*, 2001). The degree to which vicariance has contributed to the currently observed distribution patterns has long been debated, but the increasing availability of dated molecular phylogenies now allows a more comprehensive overview of the relative importance of vicariance versus dispersal. At the level of species or species pairs, a number of intercontinental disjunctions that have formerly been attributed to vicariance events have now been shown by molecular studies to be so recent that long distance dispersal is more likely (e.g., Moran and Smith, 2001; Kreier and Schneider, 2006; Janssen *et al.*, 2007). In contrast, deep phylogenetic splits may be as old as or even older than the breakups between the continents. For example, the separation of the

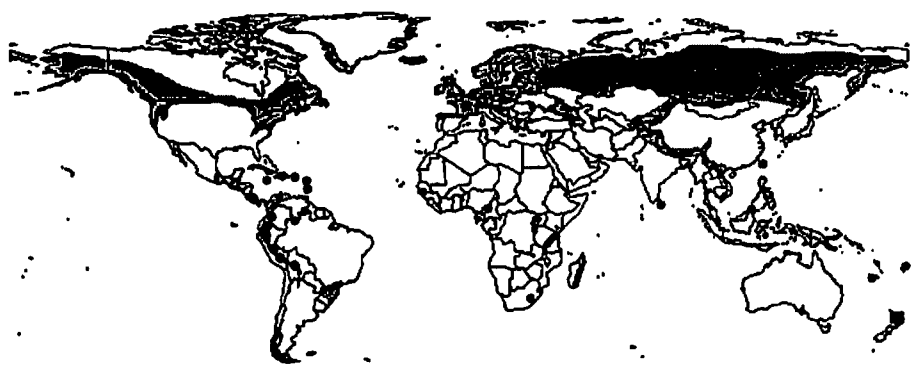

Fig. 2.1 Distributions of *Lycopodium clavatum* (gray shading), one of the most widespread lycophyte species (albeit with several subspecies and varieties, some of which may be independent species), as well as the fern species *Loxoma cunninghamii* (black square) and *Loxsomopsis pearcei* (black circles), the only two members of the highly disjunct and localized family Loxomataceae.

lycophyte genus *Huperzia* (fir-moss, Plate 3C) into a New World and an Old World clade is estimated to have taken place before the separation of Africa from South America some 95 mya (Wikström and Kenrick, 1997, 2000, 2001), followed by more recent dispersal events of younger subclades between the continents (Wikström *et al.*, 1999). Similar cases of deep phylogenetic splits between Old and New World clades that may be attributed to vicariance are found in Blechnaceae (Cranfill and Kato, 2003), Cyatheaceae (Conant *et al.*, 1995; Korall *et al.*, 2006), Isoëtaceae (Hoot *et al.*, 2006), Hymenophyllaceae (Dubuisson *et al.*, 2003), Polypodiaceae (Ranker *et al.*, 2004; Schneider *et al.*, 2004a) and *Polystichum* (sword fern; Little and Barrington, 2003). As a result of these deep phylogenetic splits, and despite numerous cases of long distance dispersal, much of the fern diversity of the New and Old World tropics has evolved independently of each other. For example, the fern floras of Mount Kinabalu in Borneo and Carrasco National Park in Bolivia, each with about 600 species, probably share no more than 60 ancestors between both areas (Kessler *et al.*, 2001).

The fern floras of the four major vegetated landmasses of the southern hemisphere provide other case studies for the relative roles of dispersal and vicariance. At least 103 species occur on two or more of the southern continental regions, including 13 present in South America as well as Australia (including New Zealand; Parris, 2001). New Zealand has been separated from other mainland areas about 80 mya and because some major fern lineages are much older than this, it was proposed that vicariance played an important role in determining the composition of its fern flora (Copeland, 1939; Lovis, 1959). However, recent fossil, distributional and cytological data now favor dispersal (Pole, 1994; Brownsey, 2001). Molecular studies of 31 genera have shown that, in the majority of cases, divergence times from the most closely related relatives studied were very short, supporting long distance dispersal into or out of New Zealand (Perrie and Brownsey, 2007). However, determination of the age of phylogenetic lineages is often problematic, because of the difficulty of finding reliably dated fossils or geological events, and because of varying rates of molecular substitution (Bromham and Penny, 2003). In the case of New Zealand, in three to six cases (depending on the parameters chosen for the analysis) divergence times were long enough to be in accordance with both vicariance and dispersal.

At a different spatial and temporal scale, vicariance can also be caused by climatic shifts that influence the distribution of vegetation types. In particular, glacial events have shaped distribution patterns of many species, especially in temperate and high montane regions. In New Zealand, for example, *Asplenium hookerianum* is currently widespread on both main islands, but genetic studies

suggest that during the ice ages this species was distributed in scattered populations, often close to the ice shields (Shepherd *et al.*, 2007). In Europe, diploid populations of some species of *Asplenium* (spleenwort) are restricted to the southern Alps, presumably corresponding to refugial populations formed during glacial periods, whereas the tetraploid forms are found over large areas of Central Europe, but colonized these regions only in the last *c.* 10 000 years (Trewick *et al.*, 2002).

2.3 Range size: variability and spatial distribution

2.3.1 Range size and its correlates

Fern and lycophyte species, genera and families are on average more geographically widespread than flowering plants (Tryon, 1970, 1986; Smith, 1972). This is most likely due to their efficient spore dispersal, but other interpretations have also been proposed (see Section 2.2.3; Smith, 1993; Wolf *et al.*, 2001). It was long believed that fern and lycophyte taxa are older, with some of them predating the major continental drift events. This is certainly the case for the older fern families such as Dicksoniaceae, Gleicheniaceae, Hymenophyllaceae, Osmundaceae and Schizaeaceae whose lineages are 150–300 million years old, but most modern families have arisen at the same time as, or even after, many angiosperm families (50–100 mya, Schneider *et al.*, 2004a). It is also conceivable that ferns may evolve more slowly than angiosperms due to differences in reproductive biology and ecology (Smith, 1972).

Distributional ranges of individual fern species vary by many orders of magnitude. Among the most widespread fern species are *Cystopteris fragilis* (brittle fern) and *Lycopodium clavatum* (common club-moss) that occur almost throughout temperate regions and tropical montane ecosystems (Fig. 2.1). At the other end of the scale are species known from single populations with few individuals. Examples include *Isoëtes tennesseensis* (quillwort), known only from two small rivers in southeastern Tennessee (Luebke and Budke, 2003), and *Asplenium tunquiniense* which is locally common in about 1 km² of cloud forest in Bolivia, but absent in nearby areas (Kessler and Smith, 2006).

The range of a species is determined by its age, its ecological requirements, the availability of suitable habitats and the ability of the species to reach these habitats and survive there (Lester *et al.*, 2007). Ranges of ferns are usually considered to be more strongly determined by habitat availability than by their, generally high, dispersal capability (Tryon, 1970, 1986; Smith, 1972, 1993; Richard *et al.*, 2000; Guo *et al.*, 2003; Tuomisto *et al.*, 2003a, 2003b; Jones *et al.*, 2006). The efficiency of spore dispersal can be illustrated by the uniformity of haplotypes among some ferns in the northern hemisphere (e.g., *Asplenium*

viride, green spleenwort, James *et al.*, 2008). However, there is also some evidence for limitations on dispersal such as for several calcicolous ferns (i.e., species that thrive on calcareous soils) in Canada that are absent from what are apparently environmentally suitable microsites (Wild and Gagnon, 2005).

On a different spatial scale, Moran (1995, 1996) estimated that nearly 25% of the fern species in Colombia and Ecuador on the western side of the Andes do not occur on the eastern side, suggesting that the mountains have acted as a barrier to migration, although environmental differences between the slopes may also play a role. Limitations on dispersal are more likely to play a role in species with highly specific habitat requirements and small, isolated patches of suitable habitat (Peck *et al.*, 1990).

Range size may also be correlated with other reproductive and morphological traits. Among Japanese ferns, for example, ranges are larger in species with multiple reproductive modes (sexual + vegetative or apogamous) than in species with a single mode (Guo *et al.*, 2003). The same study showed that while diploid species display wide variability in range sizes, polyploid species uniformly had small ranges, possibly as a result of the relatively young age of species derived from polyploidization. Interestingly, these findings contrast with the observations on *Asplenium* in Europe where diploid taxa often are glacial refugees (Trewick *et al.*, 2002). Similarly, in *Pellaea* (cliff brake), polyploid derivatives have been assumed to start out with small ranges but often eventually outcompeted their diploid progenitors (Tryon, 1957). Further, in Japan seasonally green species have larger ranges than evergreen species, presumably due to limited subtropical habitat suitable for evergreen species (Guo *et al.*, 2003). In Bolivia, latitudinally widespread fern species also tend to have broader elevational ranges, implying that they are ecologically more adaptable than localized species (Kessler 2002b). On the other hand, in a Bolivian cloud forest, fern species with restricted ranges tend to be locally more frequent than widespread species, which may be due to more specific adaptations of localized species to specific habitats, although a sampling bias (widespread species have more distribution gaps and are therefore on average less frequent) cannot be excluded (Kessler, 2002b). Contrary to the Japanese study (Guo *et al.*, 2003), range size of Bolivian ferns was neither correlated to life form nor to the studied reproductive aspects (sexual versus asexual reproduction, spores with chlorophyll versus spores without chlorophyll; Kessler, 2002b).

2.3.2 Endemism

Endemic plant species (i.e., species with restricted ranges) are not randomly distributed. They are especially well represented on oceanic islands (Carlquist, 1974), in isolated habitats such as mountain ranges (Humphries, 1979; Gentry, 1986), on

localized geological substrates (Kruckeberg and Rabinowitz, 1985; Cowling *et al.*, 1994) and in tropical and subtropical regions (Gentry, 1986; Stevens, 1989). Considering ferns, geographically isolated islands are well known for their high levels of endemism as exemplified by the 77% endemic fern species in Hawaii (Palmer, 2003). This can be explained by rare colonization events resulting in initially small, genetically isolated populations that can diverge quickly from their source populations through genetic drift, bottleneck effects or adaptation and selection.

Along elevational gradients, patterns of endemism are less easily explained. Concentrations of endemic fern species are generally found at high elevations, typically above the peak of total species richness (Fig. 2.2; Tryon 1972; Kessler, 2000b, 2002b; Kluge and Kessler, 2006). This distribution is probably influenced by a more subtle kind of geographical isolation. Mountains are typically steepest at high elevations (Körner, 2000). As a result, species with given elevational

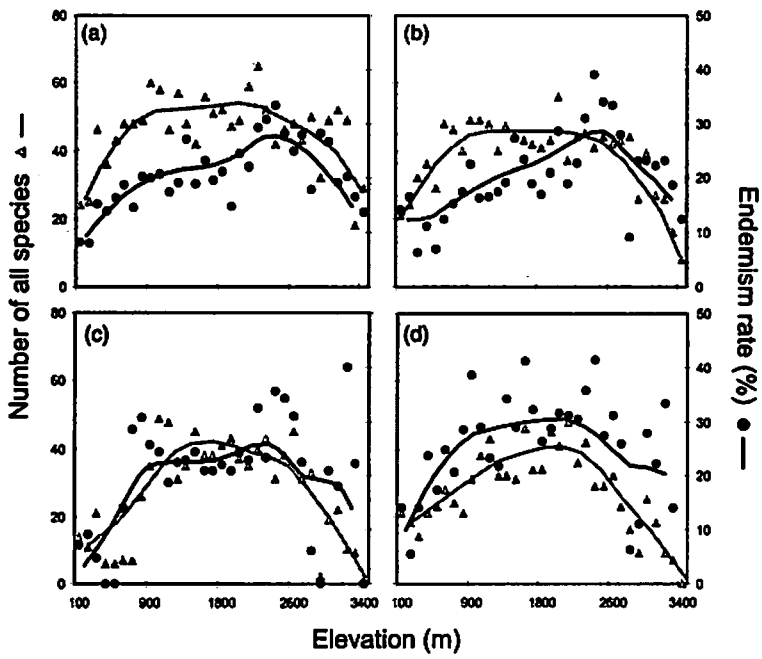

Fig. 2.2 Patterns of species richness and rates of endemism (% of endemic species) of (a) all fern species, (b) terrestrial species, (c) trunk epiphytes and (d) high-canopy epiphytes in plots of 400 m^2 along an elevational gradient in Costa Rica. (Modified after Kluge and Kessler, 2006.) For this analysis, species are considered to be endemics if they are restricted to Costa Rica and Panama (24% of all fern species recorded in this study). Note that while overall the peak of endemism is located at higher elevations than that of species richness, this pattern is primarily caused by the terrestrial species. The trend lines in this figure were drawn by distance-weighted least-squares smoothing and are intended to guide the eye.

amplitudes have narrower (and steeper) ranges at high than at low elevations. For example, a species occurring in cloud forest at 2500–3500 m on the eastern Andean slope from Venezuela to Bolivia will have a range that is 600 times longer than wide, whereas at 500–1500 m this ratio will be less than 100 (Graves, 1988). Such narrowly linear ranges are not conducive to gene flow, resulting in genetic fragmentation between populations, and eventual speciation (Kessler, 2002a). However, the story does not end here. In Costa Rica, fern endemism is not highest at the topographically steepest and most fragmented elevations, but rather at somewhat lower elevations with higher humidity, suggesting that species formation and survival may be favored there (Kluge and Kessler, 2006). Even more interestingly, species of different life forms and habitats show distinct patterns (Fig. 2.2). For example, maximum endemism of crown epiphytes is found at lower elevations than for trunk epiphytes and terrestrial species (Kluge and Kessler, 2006). The causes for these distinct patterns are unknown.

Species with small ranges are generally considered to be of particular conservation concern because their small ranges render them particularly susceptible to habitat loss (Balmford and Long, 1994) and to human-induced habitat disturbance (Moolman and Cowling, 1994; Samways, 1994; Andersen *et al.*, 1997). Comparing natural and strongly degraded habitats (Kessler, 2001a; Paciencia and Prado, 2005), this is certainly true for ferns. However, two studies in Bolivia suggest that endemic ferns may profit, in terms of diversity, from slight habitat disturbance. In one study, the relative abundance of ferns at 16 sites was higher in forests with a low level of human disturbance (through logging or cattle grazing) than in nearby undisturbed forests (Fig. 2.3A; Kessler, 2001a). A second study showed that along a chronosequence of vegetation succession on landslides, fern communities in senescent (i.e., decaying) forests were less species-rich and more strongly dominated by widespread species than communities in mature (i.e., climax) forests (Fig. 2.3B; Kessler 1999). The relationship between range size and competitive ability may be explained by the difficulty less competitive species have in expanding their ranges, whereas strong competitors have a higher probability of establishing new populations following medium to long distance dispersal. Thus, species with small ranges might be competitively inferior to widespread species. Further, localized species may depend on a certain level of habitat disturbance that disrupts competitive interactions and thus limits their competitive exclusion by widespread species. Under natural conditions, disturbance regimes may be high enough to allow the persistence of the localized species but perhaps below their optimum level. In contrast, high levels of human disturbance often lead to massive losses of species (Kessler, 2001a). Clearly, intriguing questions for future research include the relationship between range size and dispersal, competitive ability and taxonomic affinity of ferns.

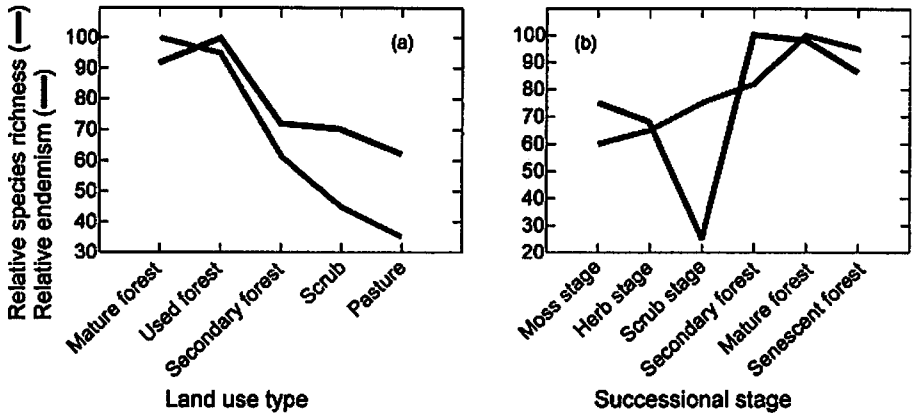

Fig. 2.3 Patterns of species richness (gray lines) and rates of endemism (black lines) of ferns in plots of 400 m^2 along (a) a gradient of human vegetation degradation and (b) a gradient of vegetation succession on landslides (modified after Kessler, 1999 and 2001a). Note that endemism is highest in forest used by humans for timber extraction and cattle grazing as well as at intermediate stages of vegetation succession, suggesting that localized species are competitively rather weak.

2.4 Alpha diversity

2.4.1 Patterns of species richness

The total number of known ferns is estimated at about 9600 species worldwide (see Appendix A; Smith *et al.*, 2006), plus about 1400 lycophytes. However, about 100 "new" species are being described yearly and the total number of species may be closer to 15 000 (Roos, 1996; Chapman, 2006). "New" species are recognized both as a result of intensive collection activity, especially in remote tropical regions and through detailed taxonomic studies. For example, about 110 fern species, 9% of the currently known Bolivian fern and lycophyte flora, have been described from Bolivia in the last ten years (e.g., Lehnert, 2006; Kessler and Smith, 2007). Of these, roughly two thirds are based on specimens first gathered in the last two decades, whereas the other third represents species already collected and present in herbaria but not recognized as distinct new taxa until recently. The number of Bolivian fern and lycophyte collections and known species increased exponentially from 881 collections and 404 species by 1970 to 4207 collections and 743 species by 1990, and to 23 221 collections and 1165 species by 2006. When this collecting activity is mapped using grid cells, it emerges that 95% of all collections come from less than 5% of the Bolivian territory. However, even the most densely sampled area in Bolivia, with 2270 samples representing 401 species in about 700 km^2, is still incompletely known, and statistically we infer that at least

560 species should be expected there. Importantly, the degree of undersampling is more pronounced in the species-rich grid cells, even if the number of collections is higher (Soria-Auza and Kessler, 2008). We can conclude that our knowledge of the spatial distribution of ferns at global and regional scales is still far from complete and that it is biased toward the better studied, species-poor areas because of greater undersampling in species-rich regions. Of course, this does not only apply to Bolivia but also to many other tropical regions such as the Andes, Madagascar and Southeast Asia, which probably have the least well known fern floras.

Despite problems in obtaining accurate species counts, the diversity of ferns varies to such a degree among regions and habitats that broad patterns of diversity are clearly discernible. Fern communities are richest in wet tropical regions, particularly in cloud forests. A global analysis of fern diversity, based on data from 205 mainland and 117 island floras, has only recently been conducted (Plate 1A; H. Kreft, unpublished data). The analysis confirmed that fern richness is highest in regions with high potential evapotranspiration, (i.e., a measure of how much water vaporizes or is transpired per year), a high number of rainy days and marked topographical relief (i.e., mountains). This largely corresponds to results obtained from regional studies, most of which find that the species richness of ferns is primarily determined by the level of rainfall and topographic complexity (Rwanda: Dzwonko and Kornaś, 1994; Bolivia: Kessler, 2000b; Iberian Peninsula: Pausas and Sáez, 2000, Ferrer-Castán and Vetaas, 2005; New Zealand: Lehmann *et al.*, 2002; Australia: Bickford and Laffan, 2006). The only known exception is Uganda, where fern diversity at a local scale is primarily determined by soil fertility and the distance from putative Pleistocene forest refugia (i.e., forest-covered areas during the ice ages; Lwanga *et al.*, 1998). Whether it is a natural phenomenon that climate is more important globally and soils at a local scale, or whether there is a methodological bias remains to be explored. Data for soil nutrients have been rarely considered, because they are more difficult to obtain for large geographic areas than climate data.

While the overall diversity pattern of ferns coincides with that of seed plants (Barthlott *et al.*, 2005; Kreft and Jetz, 2007), there are some marked differences (Kramer, 1993; H. Kreft, personal communication). Whereas seed plants are highly diverse in regions with Mediterranean-type climates (hot, dry summers and cool, wet winters), and moderately diverse in arid regions, ferns are generally species-poor in these habitats, although some groups such as *Selaginella* (spike-moss, Plate 3B), cheilanthoid ferns (Fig. 5.1c), and the *Asplenium aethiopicum* complex are represented by numerous species. Furthermore, the latitudinal increase of species numbers from the poles toward the equator is 2–3 times steeper for ferns than for seed plants (H. Kreft, personal communication). Clearly, the range of

climatic conditions under which ferns can occur and could diversify is more limited than the range for seed plants, with the exception of epiphytic ferns. These extend farther into cold habitats than any epiphytic flowering plant group both in temperate regions (e.g., *Polypodium*, Zotz, 2005) and in high tropical mountains (e.g., *Melpomene*, Krömer *et al.*, 2005). Also, along with some bromeliads, ferns of the genus *Pleopeltis* (Fig. 5.1e, Plate 7C) are among the vascular epiphytes reaching farthest into dry habitats in the neotropics. Interestingly, these three genera all belong to the family Polypodiaceae, suggesting that familial traits within this phylogenetically derived family support resistance to extreme climatic conditions.

In addition to patterns of absolute species numbers, one may focus on the relative contribution of ferns to the vascular plant flora in different geographical regions or habitats. Worldwide, ferns comprise an average of 3.6% of different vascular plant floras (H. Kreft, personal communication.). However, in tropical forests and in montane habitats they can represent up to 13% of the local flora, whereas in desert regions they may be completely absent. On islands, ferns on average represent about 15% of the local vascular plant species, and in exceptional cases up to 70% on islands such as Easter Island, Palau, Saint Helena and Tristan da Cunha (Plate 1B). The proportion of fern taxa typically increases with the distance of the islands from the mainland, undoubtedly as a result of the higher dispersal ability of ferns compared with most seed plants. However, this relationship is not perfect, and some remote islands have fewer ferns than expected. Examples are the cold, windswept Falkland Islands, and especially flat and mountainless tropical atolls such as the Maldives that lack habitats suitable for most ferns.

Within the global framework of fern diversity, mainland Africa is particularly poor in fern species. Whereas the neotropics and Southeast Asia both have in the order of 3000–4500 species, mainland Africa has only about 630 species (Tryon, 1986). Even Madagascar, which is 40 times smaller than mainland Africa, has about 560 species. This pattern has been explained by the limited surface area of humid tropical mountains in Africa (Moran, 1995). However, in the global analysis (H. Kreft, personal communication), Africa has fewer species than expected under present-day conditions, even when all climatic and landscape factors (including area and topographic relief) are considered. This low diversity of African ferns may thus be best explained by Pleistocene climatic oscillations, during which rainforests in Africa were restricted to small refugia, while most of the continent was covered with drier vegetation types, presumably leading to widespread extinctions of ferns (Kornaś, 1993). A detailed analysis of distribution patterns of African ferns has shown that these can be separated into three main groups that correspond to refugial areas (Aldasoro *et al.*, 2004): Guinea–Congolian thermophilous species inhabit the lowland rain forests of West and Central Africa and had their refuge around the Gulf of Guinea; the cold-tolerant, Afro-montane

taxa survived the dry periods mainly in the East African mountains; and the southern drought-tolerant elements had their refuge in the Cape Region.

2.4.2 Mountains as hot spots of fern diversity

Tropical mountains are clearly the hot spots of fern diversity. A number of studies have shown that on high tropical mountains, species richness shows a hump-shaped elevational richness pattern, with highest diversity at mid-elevations and decreasing diversity toward both high and low elevations (Fig. 2.4; Jacobsen and Jacobsen, 1989; Parris *et al.*, 1992; Kessler, 2000b, 2001b, 2001c, 2002a; Kessler *et al.*, 2001; Hemp, 2002; Bhattarai *et al.*, 2004; Kluge *et al.*, 2006; Watkins *et al.*, 2006). The elevation at which maximum fern diversity occurs differs somewhat among mountain ranges, with maxima at about 1800 m in both Costa Rica (maximum mountain height 3820 m, Kluge *et al.*, 2006) and on Mount Kinabalu, Borneo (4000 m, Kessler *et al.*, 2001), at 2000 m in Bolivia (4500 m, Kessler, 2000b), and at 2400 m on Mount Kilimanjaro, Tanzania

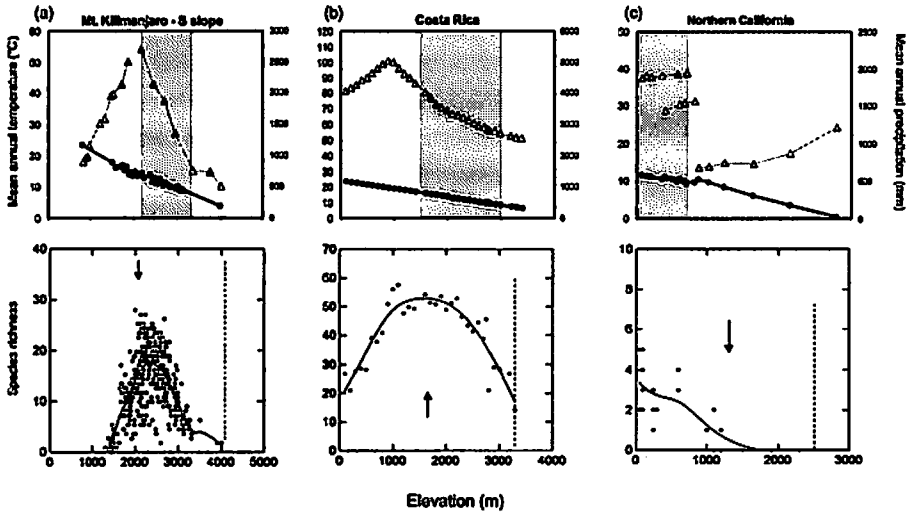

Fig. 2.4 Elevational patterns of climatic variables (top row) and fern species richness (bottom row) in (a) Tanzania (after Hemp, 2002), (b) Costa Rica (after Kluge *et al.*, 2006) and (c) California (M. Kessler, unpublished data). In the climate figures, left axes and dotted lines show values of mean annual temperature; right axes and triangles mean annual precipitation; elevational steps with extensive occurrences of fog ("cloudbelts") are shaded gray. In the species richness figures, dashed vertical lines show the natural upper limits of the study gradients (timberline or mountain peaks), and arrows the elevational midpoints of the gradients. Note different scales of axes. The trend lines in this figure were drawn by distance-weighted least-squares smoothing and are intended to guide the eye.

(5850 m, this volcano is placed on a plateau at about 1000 m, Hemp 2002). In temperate regions such as New Zealand (Ohlemüller and Wilson, 2000) or North America (Fig. 2.4), richness may decline continuously with elevation or remain roughly constant. Climatically, these gradients correspond to the upper parts of tropical gradients, where richness also declines, and indeed species numbers are comparable between these data sets at similar values of mean annual temperature (M. Kessler and J. Kluge, unpublished data). The maxima of fern richness have often been interpreted as reflecting the elevation of maximum humidity (Kessler, 2001a; Hemp, 2002) or an optimal combination of humidity and mild temperatures (Bhattarai *et al.*, 2004; Kluge *et al.*, 2006). For example, in South America a number of fern species that typically occur along the lower slopes of the Andes extend into the wettest part of the Ecuadorian Amazon basin, suggesting that the lower elevational limit of these species is determined by environmental humidity (Kessler 2001b).

At an even finer spatial scale, fern richness typically is higher in humid microhabitats (Richard *et al.*, 2000), in ravines, and along streams rather than on slopes, and lower on mountain ridges than on slopes (Kessler, 2002b; Kluge and Kessler, 2006). Again, this has been linked to the higher and more constant humidity close to water bodies, although higher soil fertility on lower slopes and near streams may also play a role.

2.4.3 Mechanisms determining patterns of species richness

Area dependence of species richness

Area is a crucial parameter determining biodiversity patterns for all taxa, because larger areas can support higher numbers of individuals and hence more viable populations of a larger number of species, reducing extinction risks (Rahbek, 1995; Rosenzweig and Ziv, 1999; Lomolino, 2001). Furthermore, larger areas typically contain a wider range of habitats. While the influence of area on fern richness is obvious when we compare countries (Plate 1B) or islands (Roos *et al.*, 2004) of different sizes, it is much less clear-cut on mountains, where area per altitudinal belt typically declines with elevation (Körner, 2000), but where fern richness peaks at mid-elevations. On mountains, other factors, in particular climate, play a primary role.

Climate dependence of species richness

It has frequently been noted that most ferns are particularly water-dependent plants that require high humidity for their growth and their reproduction (e.g., Tryon, 1976; Barrington, 1993); this is because gametophytes depend on water

for the transport of gametes, and because some of the conspicuous adaptations to water stress among flowering plants (e.g., succulence, annual life cycle) are rare or absent among ferns. This reasoning may involve circular argumentation, however, because the "optimal" conditions are defined by where the largest number of species is found rather than on where environmental conditions are truly optimal for fern development, both relative to environmental conditions and to interactions with other plants. Furthermore, ferns are not totally absent in many relatively inhospitable habitats, and many fern and lycophyte lineages have evolved morphological adaptations to deal with water stress, low temperatures or both (see Chapter 5; Pickett, 1931; Gaff, 1977; Kramer *et al.*, 1995; Page, 2002; Kessler *et al.*, 2007). If these drought-adapted species can survive under these relatively adverse conditions, why are there so few species?

There are two fundamentally different ways in which the number of coexisting species in a given habitat can be limited: by actual local environmental conditions such as energy availability or by historical factors.

Local limitations of species richness

Favorable climatic and soil conditions allow the growth and persistence of a larger number of individuals of a given higher taxon, in our case ferns. Accordingly, the energy available through primary production to the fern communities for growth and reproduction is higher under favorable conditions. The species-energy theory states that the more energy that is available in an ecosystem, the more species will be able to coexist (Wright, 1983). Indeed, indirect measures of energy availability at the ecosystem level such as AET (actual evapotranspiration) or PET (potential evapotranspiration) are often positively related to plant species richness (Kreft and Jetz, 2007; H. Kreft, personal communication). However, there are two challenging aspects in addressing the species–energy relationship. The first is to get the appropriate measure for energy availability. The theoretical relationship of species richness to energy availability is based on net primary productivity (NPP, i.e., the amount of energy fixed by plants through photosynthesis and made available to the plants themselves and to the consumers). Yet, because NPP is difficult to measure, field studies usually use surrogates of NPP such as AET, PET, vegetation biomass, or tree growth (Waide *et al.*, 1999). However, none of these measures gives a reliable estimate of NPP, and Waide *et al.* (1999) have concluded that there are no studies "relating diversity directly to productivity". Secondly, measures of NPP at the ecosystem level may be quite meaningless for specific study groups such as ferns. In a forest ecosystem, most of NPP is contributed by the trees, whereas ferns only contribute a small and variable percentage. Clearly, in order to address the species–energy relationship for ferns, we first need measurements of the productivity of fern species. Such data are completely lacking at present.

Moreover, even less is known about the mechanisms that may answer the question "how can increasing energy materialize into more species?" (Willig *et al.*, 2003; Mönkkönen *et al.*, 2006). Until recently, literature on species richness–energy relationships referred only in very few cases to such causal mechanisms, probably because of the belief that they were understood. For example, Rosenzweig and Abramsky (1993) stated that the relationship between richness and energy "troubles no one": a poor environment does not provide many resources for rare species, and they become extinct. This simplistic view has proven to be misleading, as the few studies addressing this relationship report conflicting results (Willig *et al.*, 2003; Evans *et al.*, 2005). Most recently, the set of potential mechanisms that may explain the causality of the species–energy relationship has been reviewed by Evans *et al.* (2005). They evaluated nine hypotheses, three of which may apply directly to ferns and are discussed below to provide an impression of their theoretical background and the data needed to evaluate them.

The *population size hypothesis* basically postulates that increasing energy may support more individuals and thus more species. This idea is analogous to the Theory of Island Biogeography, in which species richness increases with area because larger areas support more resources (but only in total, not necessarily per unit area) and thus more individuals, enabling species to maintain higher population sizes and to reduce extinction risks (MacArthur and Wilson, 1967). Replacing "area" by "energy availability", indicates that high energy areas support more species by shifting population sizes above the threshold of viability (Kaspari *et al.*, 2000; Hurlbert, 2004; Pautasso and Gaston, 2005, 2006). This hypothesis predicts that along a gradient of species richness, the number of individuals per species, or at least the minimum number of individuals per species needed to maintain viable populations, should remain roughly constant, if species assemblages were saturated. In contrast to this assumption, the number of fern individuals per species increases in Costa Rica with elevation in survey plots of constant size (Fig. 2.5; J. Kluge and M. Kessler, unpublished data). This may suggest that at high elevations, fern communities do not reach their maximum species diversity because the occurring species are overrepresented by more individuals than needed to maintain their populations, leaving no room for the immigration of additional species. However, the vegetative size of fern individuals also declines with elevation (Kessler and Siorak, 2007; Kessler *et al.*, 2007; Kluge and Kessler, 2007), and it may simply be the case that at lower elevations the density of individuals is limited by their spatial requirements. And finally, we know nothing about the potential competition of ferns with seed plants at different elevations. Clearly, we have not even started to properly address these topics.

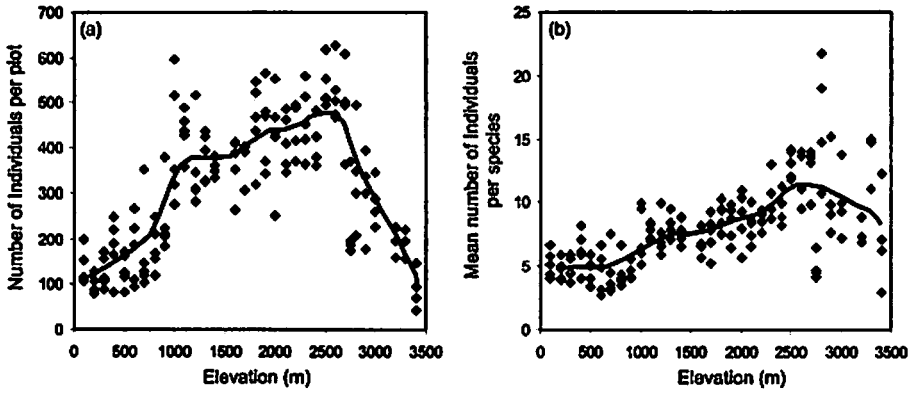

Fig. 2.5 (a) Total number of fern individuals and (b) mean number of individuals per species along an elevational gradient in Costa Rica (J. Kluge and M. Kessler, unpublished data). Compared with the pattern of species richness (Fig. 2.2A), the peak of number of individuals is located at higher elevations, resulting in an overall increase of individuals per species. The trend lines in this figure were drawn by distance-weighted least-squares smoothing and are intended to guide the eye.

The *niche position hypothesis* proposes that niche position specialists use relatively specific, rare resource types that may be too scarce in low energy areas to allow the survival of viable populations (Abrams, 1995). Thus, the niche position hypothesis provides a causal link between energy and habitat heterogeneity (Hurlbert and Haskell, 2003; Hurlbert, 2006). The central prediction is that energy input determines the variety and abundance of resources and thus population sizes of species specialized on certain resource types; in high energy areas, rare resource types are more likely to support viable populations than in low energy areas. This hypothesis has never been tested for ferns.

In contrast, the *niche breadth hypothesis* assumes that when resource abundance increases, species may switch from a wide array of resources to their preferred ones, leading to reduced niche breadth in high-energy areas. This restriction may lead to reduced niche overlap and hence lower competition, promoting coexistence. The diagnostic prediction of the niche breadth hypothesis is that along gradients of energy input, species have their widest niche breadth at the end of lowest energy. For example, along an elevational transect in Costa Rica, epiphytic ferns at lower elevations usually occur only in specific parts of trees (e.g., trunk, thick branches, outer branches), whereas close to the tree line they usually grew on most parts of the trees (J. Kluge and M. Kessler, unpublished data). This may suggest that niche breadth increases, but also that the environmental conditions on tree trunks and in the canopy are much more similar to each other in stunted forests close to timberline than in a 40 m tall forest in the lowlands. Microenvironmental measurements at the actual growth sites of the species are needed to evaluate the niche breadth hypothesis for ferns.

These few examples should suffice to give an idea how local energy availability may limit the richness of fern assemblages. We can conclude that while the theoretical framework is reasonably well established, empirical studies do not yet exist, and that the methodological hurdles in testing these hypotheses will be high.

Historical limitations of species richness

Gradients of richness are not static, and present-day patterns can be seen as a snapshot of a dynamic history on a very large temporal scale (e.g., Wiens and Donoghue, 2004; Ricklefs, 2005; Roy and Goldberg, 2007). A classic example is the low diversity of African ferns that is attributed to adverse climatic conditions in the past, which have led to extinction of ferns or reduced possibilities for their diversification. On other continents, the diversity of ferns may have experienced similar historical limitations or perhaps reached a maximum determined by the carrying capacity of the ecosystems. Given enough time and suitable environmental conditions for future diversification, fern richness may continue to increase differentially over evolutionary time and result in diversity patterns different from those observed today.

There are several ways in which historical factors may influence patterns of diversity (Wiens and Donoghue, 2004; Allen and Gillooly, 2006; Mittelbach *et al.*, 2007; Ricklefs, 2007). For example, the tropics may harbor a higher diversity than temperate regions because the taxa under consideration, in our case the major phylogenetic lineages of ferns, have originated there, and adaptations necessary to disperse and persist in cold and climatically seasonal regions have evolved only in some taxa and at a later point in time (niche conservatism *sensu* Wiens and Donoghue, 2004). Humboldt (1808) proposed that high latitudes support fewer species because they have to tolerate low temperatures, a line of thinking leading to Currie *et al.*'s (2004) "climatic tolerance" hypothesis. Tropical regions had a greater extent in the historical past (Behrensmeyer *et al.*, 1992), and many extant clades are originally tropical, leading to greater time and space availability for speciation under tropical conditions. Alternatively, regions with lower present-day diversity may have suffered from more pronounced extinction events, as suggested above for Africa. These two hypotheses are based on the assumption that rates of diversification are similar in all geographical regions and that the differences in species richness are the consequence of the time available for diversification and differing rates of extinction (Mittelbach *et al.*, 2007; Ricklefs, 2007). However, rates of diversification may differ between regions or habitats, because of higher mutation rates and shorter generation times in high energy areas (Evans *et al.*, 2005). This mechanism predicts that mutation rates are directly linked to solar energy by temperature and ultraviolet radiation and indirectly by reduced generation time, although few studies have shown such a positive relationship (e.g., Cardillo, 1999).

These potential historical explanations have not yet been explicitly tested for ferns or for most major groups of organisms (Wiens and Donoghue, 2004; Ricklefs, 2005; Harrison and Cornell, 2007). It has been proposed that ferns have lower diversification rates than flowering plants, either due to the lack of many of the isolating mechanisms found in angiosperms, or due to higher levels of gene flow between populations (Tryon, 1970; Smith, 1972; Ranker *et al.*, 1994, 2004). Within the ferns, several recent molecular studies have shown that different clades often have distinct rates of molecular diversification (Pryer *et al.*, 2001; Schuettpelz and Pryer, 2006), perhaps as a result of alterations in life cycles and reproductive biology linked to ecological adaptations (Haufler *et al.*, 2000; Bromham and Penny, 2003), or due to genome-wide shifts in the rates of nucleotide substitutions (Schuettpelz and Pryer, 2006), although there is no direct evidence for either of these explanations. Schneider *et al.* (2004b) found that the deeper branches of the asplenioid fern diversification correspond to a division into tropical and temperate clades, with temperate clades evolving on up to six different occasions from tropical ones. Although no statistical analyses have been conducted to ascertain if the lower diversity of asplenioid ferns in temperate regions may be attributed to later or slower diversification or to higher extinction, the overall pattern found by Schneider *et al.* (2004b) certainly suggests that evolutionary processes played a role in shaping present-day diversity patterns in this fern lineage. Comparing radiations of several genera of Polypodiaceae, Haufler *et al.* (2000) suggested that in temperate regions fern speciation may be primarily driven by allopatry (i.e., divergence of geographically separate populations), whereas in the tropics, ecological specialization and sympatric speciation may predominate. Similar thoughts were developed by Yatabe *et al.* (2001) for the diversification of Asian species of *Asplenium*. This interesting hypothesis remains to be tested more thoroughly.

On a different timescale, Schneider *et al.* (2004a) have shown that most of the contemporary fern diversity evolved after the main diversification of angiosperms in the Late Cretaceous and Early Tertiary. They proposed that flowering plants profoundly changed the habitat conditions, especially in forest ecosystems, from fern- (and gymnosperm-) dominated forests with an open vegetation structure and much light reaching the ground level to denser and darker angiosperm-dominated forests. Fern groups that have managed to adapt to these new conditions, e.g., through the development of more sensitive photoreceptors that allow sufficient photosynthesis even under low light conditions (Schneider-Pötsch *et al.*, 1998; Kawai *et al.*, 2003), could then diversify in the new niche. The radiation of fern lineages may also be linked to ecological specialization as in Pteridaceae (Schuettpelz *et al.*, 2007). In this family, distinct clades are characterized by their aquatic (*Acrostichum*, leather fern and *Ceratopteris*, antler fern), epiphytic (vittarioid ferns, Plate 6D) or xeric habitats (cheilanthoid ferns, Fig. 5.1c), suggesting that ecological innovation was responsible for the initial diversification of the family.

See Chapter 5

Dispersal limitation

Species richness may not only be influenced by deterministic processes as outlined above, but also by stochastic factors and dispersal limitation. For example, the range placements of species within geographically or ecologically constrained domains may independently create patterns of species richness (Colwell and Hurtt, 1994). This mid-domain effect (MDE), a geometrical null model in which species ranges are randomly placed along a geographical domain with hard outer boundaries resulting in hump-shaped richness patterns, has been invoked as an explanation for richness patterns along elevational and latitudinal gradients (see review in Colwell *et al.*, 2004). While MDE models closely correlate with diversity patterns (especially along some elevational gradients), both for ferns (Kessler, 2000b; Watkins *et al.*, 2006) and other taxa (Colwell *et al.*, 2004; McCain, 2005), the meaning and implications of such geometric constraint models is hotly debated (Bokma and Mönkkönen, 2000; Colwell and Lees, 2000; Jetz and Rahbek, 2001; Hawkins and Diniz-Filho, 2002; Grytnes, 2003a, 2003b; Colwell *et al.*, 2004; Herzog *et al.*, 2005). The main criticism is that the frequency distribution of range sizes, which generates hump-shaped patterns in the MDE null model, exists only because of the presence of environmental gradients (Hawkins *et al.*, 2005).

On a different spatial scale, Hubbell (2001) has suggested that the occurrence and abundance of species at given sites within a larger ecoregion or habitat is influenced by dispersal limitation. This "neutral theory of biodiversity and biogeography" considers variations in the dispersal ability of species, their population size, and their immigration rate as the crucial factors determining the composition and distribution of species abundances of communities. The relative influence of these three factors over ecological factors varies with scale and study group; local scales within ecologically more homogeneous areas show a stronger effect of dispersal limitation (e.g., Dalling *et al.*, 2002; Potts *et al.*, 2002; Svenning *et al.*, 2004; Chust *et al.*, 2006), whereas at regional scales and across strong ecological gradients, the niche assembly model appears to be more applicable (e.g., Condit *et al.*, 2002; Tuomisto *et al.*, 2003c; Jones *et al.*, 2006, 2007; Ruokolainen *et al.*, 2007).

Dispersal may also modify patterns of species richness due to mass or source–sink effects (Shmida and Wilson, 1985; Pulliam, 1988). This occurs when propagules of a species are dispersed to suboptimal habitats, where they may survive but are unable to produce enough offspring to maintain self-sustaining populations. Although such sink populations have been documented in numerous individual species (Gilpin and Hanski, 1991; Wilson, 1992; Leibold *et al.*, 2004), the extent of such populations at the community level and therefore their influence on

observed richness patterns remains largely unexplored. For example, hump-shaped patterns of species richness along elevational gradients have been hypothesized to be due to dispersal of species from lower and higher elevations, resulting in highest overlap of such sink populations at mid-elevations, whereas communities at the extremes of the gradient can receive immigrants from only one direction (Rahbek, 1997; Kessler, 2000b; Lomolino, 2001; Grytnes and Vetaas, 2002; Grytnes, 2003a, 2003b; Kattan and Franco, 2004). Grytnes *et al.* (2008) assessed elevational patterns of species richness of vascular plants along four elevational gradients in Norway. They compared patterns of species richness using only fertile populations with patterns obtained when only sterile populations were considered, assuming that species recorded only as sterile individuals represent sink populations. In several cases, they found that "sterile-only" richness patterns were more strongly hump shaped than "fertile-only" patterns. They interpreted this as an accumulation of sterile sink populations at mid-elevation sourced from species mainly inhabiting either higher or lower elevations. In contrast, the extremes of the gradient can only receive sink propagules from one direction and hence have lower diversity. This supports the hypothesis that source–sink effects do indeed modify elevational richness patterns. Comparable studies have not yet been published on ferns, but recent analyses from an elevational gradient in Costa Rica clearly show that separating sterile and fertile records indeed results in distinct patterns and that dispersal-mediated population processes appear to modify patterns of species richness (Fig. 2.6; J. Kluge and M. Kessler, unpublished data).

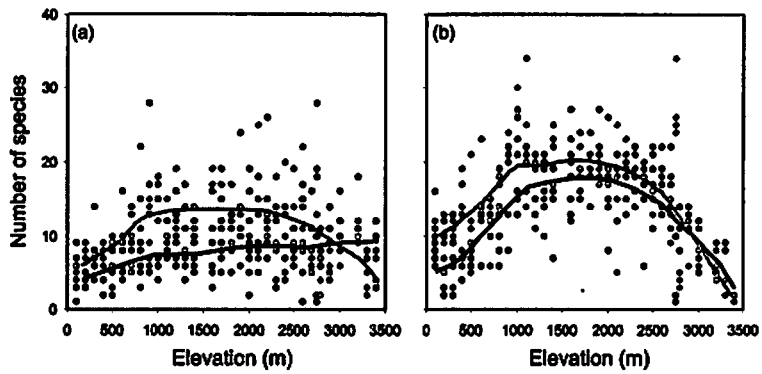

Fig. 2.6 Elevational patterns of the number of fertile (black symbols) and sterile (gray symbols) (a) terrestrial and (b) epiphytic ferns in plots of 400 m^2 along an elevational gradient in Costa Rica (J. Kluge and M. Kessler, unpublished data). Note that the hump-shaped pattern of the diversity of terrestrial ferns is caused by the accumulation of sterile species at mid-elevations. The trend lines in this figure were drawn by distance-weighted least-squares smoothing and are intended to guide the eye.

2.5 Beta diversity

Beta diversity is the change of plant or animal communities along ecological gradients. While these gradients can cover a wide range of spatial, temporal and ecological aspects, studies on the beta diversity of ferns have mostly focused on changes in geological substrates and soils as well as in elevation.

2.5.1 Soil gradients

It is well known that many species of ferns occur preferentially on specific rock or soil types. In Europe, for example, many species of *Asplenium* are restricted to either limestone, serpentine or acidic rock (e.g., basalt, granite; Vogel *et al.*, 1999b; James *et al.*, 2008). However, in most cases it is not known if their substrate specificity is based on physiological requirements, or whether it is driven by competitive interactions among species.

In the tropics, the most extensive study on the relationship of fern community composition to soil factors has been conducted by Hanna Tuomisto and colleagues in western Amazonia. They have shown that in this climatically fairly homogeneous region, differences in topography and soil conditions explain many of the changes in species composition of communities of ferns and other plant groups (Tuomisto and Ruokolainen, 1994; Tuomisto and Poulsen, 1996, 2000; Tuomisto *et al.*, 2002; Poulsen *et al.* 2006; see also Young and León, 1989). These local environmental factors appear to be overriding the effect of dispersal limitation at local (Jones *et al.*, 2006, in Costa Rica) and at regional (Tuomisto *et al.*, 2003a, 2003b, 2003c, in Amazonia) scales. Detailed studies of *Adiantum* (maidenhair fern; Tuomisto *et al.*, 1998) and *Polybotrya* (Tuomisto, 2006) in Amazonia, and of tree ferns in Costa Rica (Jones *et al.*, 2008), have likewise shown that individual species have distinct "preferences" for specific soil conditions. The specificity of fern assemblages to soil conditions renders them suitable as indicators for forest types (Ruokolainen *et al.*, 1997; Salovaara *et al.*, 2004) and for distribution patterns of other plant groups (Vormisto *et al.*, 2000). Combining these floristic studies with satellite imagery has allowed the distinction of more than 200 forest types in Peruvian Amazonia alone (Tuomisto, 1998; Tuomisto *et al.*, 1995, 2003c).

2.5.2 Elevational gradients

Along elevational gradients, the composition of fern communities changes considerably. While some major families such as Aspleniaceae and Dryopteridaceae are found from the lowest to the highest elevations, many others show

distinct elevational preferences (Mehltreter, 1995). For example, within the Hymenophyllaceae, the trichmanoid ferns typically occur at low and middle elevations (Plate 6A, B), whereas the hymenophylloid ferns are mainly found at mid to high elevations (Dubuisson *et al.*, 2003). At the species level, the restriction to specific elevational zones becomes even more apparent. Species in tropical mountains have, on average, elevational amplitudes of about 1000 m, although many occur only within a few hundred meters of altitude, and some species have wider elevational ranges of up to 3000 m (Kessler, 2002b; Kluge *et al.*, 2006; Jácome *et al.*, 2007).

While it is logical that individual fern species have specific elevational distributions determined by their ecological requirements, a more complex question is whether these elevational limits apply simultaneously to a large number of species. The latter scenario would result in a specific elevational zonation of fern assemblages that would reflect the elevational vegetation belts typically distinguished in mountains (e.g., Holdridge *et al.*, 1971; Grubb, 1974; Ellenberg, 1975; Frahm and Gradstein, 1991). Recently, a number of studies have addressed this question using statistical tests to assess if the turnover of communities at specific elevations is higher than expected by chance (Kessler, 2000a; Bach, 2004; Hemp, 2006; Bach *et al.*, 2007; Kluge *et al.*, 2008). These studies have obtained mixed results. In some cases, no distinct boundaries were found over elevational amplitudes of more than 2000 m, but in other cases, several distinct elevational zones were

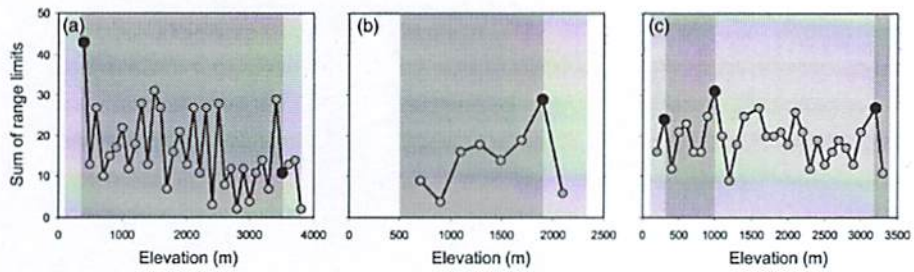

Fig. 2.7 Elevational zonation (different shades of gray) of fern assemblages along elevational gradients in the (a) very wet Carrasco National Park, Bolivia, (b) semihumid Masicurí valley, Bolivia, and (c) Costa Rica. (Modified after Kessler, 2000a, Kluge *et al.*, 2008.) The symbols show the number of species that reach their upper or lower distributional limits at a given elevation, with the black symbols denoting zones of statistically significant elevated rates of species turnover. In (a) Carrasco and (c) Costa Rica, the uppermost and lowermost two limits correspond to the transition from the lowlands to foothills and to tree line, respectively. In addition, the limit at *c.* 1000 m in (c) Costa Rica denotes the lower limit of the regular cloud condensation layer. In (b) Masicurí, the only limit shows the transition from mixed evergreen forest to forest dominated by the conifer *Podocarpus*.

discernible (Fig. 2.7). In most cases, boundaries correspond to zones where other taxa experience abrupt ecological shifts such as the upper timberline, the lower limit of the cloud condensation belt, changes in forest type (e.g., evergreen to deciduous) or the transition from the steep mountains to the flat lowlands. In many cases, floristic boundaries are determined only by accumulations of either upper or lower elevational limits of species rather than by both. For example, the abrupt shift in community composition at the lower limit of the cloud condensation belt is determined mainly by lower elevational limits of species restricted to the cloud condensation zone (Bach *et al.*, 2007; Kluge *et al.*, 2008). In the other direction, species growing at lower elevation extend to various degrees into the cloud condensation zone without presenting abrupt changes. This pattern is certainly determined by the degree to which the environmental conditions are more stressful on one side of the ecological boundary. For many fern species of the cloud condensation belt such as those of the Hymenophyllaceae, the dry conditions below it are limiting, whereas the humid conditions within the belt may not limit the range extension of any fern species of lower elevations. In conclusion, it appears that where ecological conditions change gradually, fern communities also change gradually, whereas abrupt ecological shifts lead to a distinct zonation of fern communities, with most distributional limits being directed toward the more stressful environmental conditions.

2.6 Questions for the future

While considerable progress has been made in the last few decades on the biogeography of ferns, much remains to be learned. In this review, I have discussed some of the overriding challenges to improving our understanding of fern biogeography.

At the most basic level, there is continued need for additional field surveys as well as taxonomic, systematic, and floristic studies (Smith, 2006). About 15% of all fern and lycophyte species may not yet be known to science (Chapman, 2006), and for many of those already known, information on distribution and ecology is rudimentary. Unfortunately, extensive field surveys have been restricted to the few remaining, mostly tropical ecosystems that are still unaltered. Further, climatic shifts, both as a result of global climate change (e.g., Pounds *et al.*, 1999; Still *et al.*, 1999) and of forest clearance (Lawton *et al.*, 2001), may already have disrupted the natural climate–fern community relationships. Ultimately, an understanding of the factors determining the present-day composition and diversity of fern communities will depend on linking phylogenies at species and population levels with detailed field- and laboratory-based ecological and ecophysiological measurements.

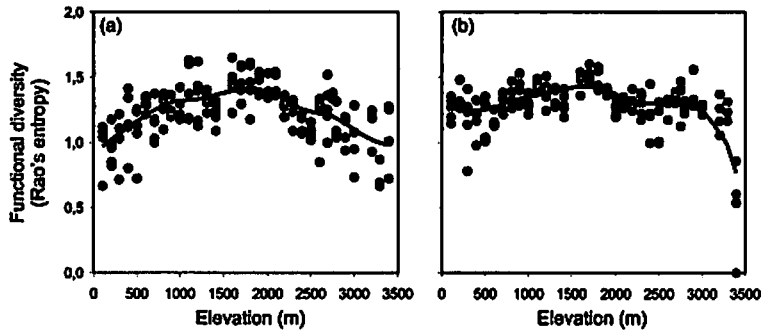

Fig. 2.8 Morphological trait diversity of terrestrial (a) and epiphytic (b) ferns along an elevational gradient in Costa Rica (J. Kluge and M. Kessler, unpublished data). The diversity index Rao's entropy gives a measure of the variability of morphological traits within a community, independently of the species richness. Note that both patterns of morphological diversity are less hump shaped than the patterns of species richness (Fig. 2.2), and that the morphological diversity of epiphytic ferns is almost constant, except above tree line, where there are only a handful of epiphytes living in scattered bushes. The trend lines in this figure were drawn by distance-weighted least-squares smoothing and are intended to guide the eye.

A deeper understanding of the population biology and genetics of ferns is indispensable in order to understand the phylogeography of many clades, and the evolution and maintenance of contemporary fern communities (Haufler, 2007). Especially for tropical taxa, questions of how the populations are spatially distributed and what levels of gene flow exist between them remain largely unexplored (James *et al.*, 2008).

In the context of community diversity, one may not only focus on species numbers, but also on the diversity of the morphological traits of the species. Thus, a community consisting of three similar species from the same genus may be morphologically less diverse than a community of three species belonging to different families and looking very different from each other (Magurran, 2004). No such studies have yet been published on ferns, but preliminary analyses along an elevational gradient in Costa Rica suggest that interesting patterns may be found (Fig. 2.8).

Finally, very little is known about the ecology and biogeography of gametophytes. Although the haploid gametophyte is a fundamentally different organism than the diploid sporophyte, there are only a few studies on the ecology of gametophytes of selected species (Cousens, 1981, 1988; Cousens *et al.*, 1985; Greer and McCarthy, 1999; Watkins *et al.*, 2007). In some of these species in which gametophytes inhabit temperate regions inhospitable to the respective sporophytes (Farrar, 1967; Peck *et al.*, 1990), the gametophytes are more stress tolerant than their sporophytes (Sato and Sakai, 1980, 1981).

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